

XIV. *On the Development of Ferns from their Spores.*By ARTHUR HENFREY, *Esq.*, *F.R.S.*, *F.L.S.* &c.

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THE remarkable discoveries published by Count Leszczyc-Suminski in 1848, together with those to which they may be supposed to have led, in the allied families of the *Cryptogamia*, in the researches of Messrs. Hofmeister and Mettenius, are of a character to excite the strongest interest among vegetable physiologists, from the important changes which they appear to necessitate in our general views of the reproduction of plants. It is certain, moreover, that they equally deserve the attention of animal physiologists, since the phenomena which have been described seem to point directly to a much closer relationship between the characters of the sexual reproduction of plants and animals, than has of late years been considered probable; for, while the facts which have been demonstrated in reference to the mode of fertilization in flowering plants seemed to remove the possibility of tracing any satisfactory analogy,—the pollen-tube differing so widely from the spermatozoon,—a new set of conditions have been revealed in plants, which present the strongest resemblance to those met with in the fertilization of animals. Still more, the remarkable biological conditions known in the Animal Kingdom under the title of ‘Alternations of Generations’ are found to occur in the Vegetable Kingdom in a much more definite manner than was supposed, presenting all the distinctness which characterizes them in animals, and by no means confined within the debateable territory in which they were at first sought, namely, in the metamorphoses of the organs of single plants.

The observations of Suminski naturally attracted the attention of the more active vegetable anatomists, and have already been repeated by several German botanists, whose results, however, not only differ in many points from those of Suminski, but also among themselves; and opinions are divided both as to the actuality of the existence of the most important point of all, viz. the process of impregnation, and as to the period and circumstances of its occurrence. Thus, while Von Merekin confirms Suminski’s statements in regard to the act of impregnation taking place at an early period, Schacht and Wigand deny it altogether; and, again, Hofmeister and Mettenius assert the fact of the impregnation of a germ-cell by spermatozoids, but declare that Suminski mistook the structure of the organs and the *modus operandi* of the phenomenon.

Under these circumstances I believed myself performing a useful task in subjecting the question to minute investigation. These researches were indeed commenced immediately after the publication of Suminski’s treatise, but were left imperfect until the past winter and the present spring, during which I have carefully repeated all my former observations, and traced the development entirely through from the spore to the young leafy plant, applying every available means to clear up the anatomical conditions in each

stage of the progress. The extreme delicacy of the young prothallium renders dissection a matter of some difficulty, and, as in the embryotomy of flowering plants, the anatomist, with all the skill acquired by practice, must be content to obtain decisive observations in but a very small proportion of his preparations:

The drawings which accompany this Memoir were nearly all made by means of the camera lucida eye-piece, so that they represent preparations actually seen; the unimportant details alone, such as the green colouring matters, &c., being given in a conventional manner, except in a few separate figures devoted to the special illustration of these points.

The first part of the Memoir is devoted to an account of my own observations; to this is added a critical examination of those of preceding authors; and, in conclusion, a few remarks on the general bearing of the results upon vegetable physiology.

As some foreign vegetable anatomists have been inclined to lay great weight on the quality of their microscopes, in discussing the points in dispute between different observers, it may be as well to state, that my investigations were made with one of Ross's large microscopes, with his 1-inch, $\frac{1}{2}$ -inch, $\frac{1}{4}$ -inch and $\frac{1}{8}$ -inch objectives (about seven or eight years old), and the drawings sketched in with the camera lucida eye-piece, after the preparations had been fully observed with various other eye-pieces. The $\frac{1}{4}$ -inch objective sufficed for most purposes; the $\frac{1}{8}$ -inch was useful for the spermatozoids, but in regard to anatomical points was chiefly used on account of the short focus, which is often advantageous where the lines of cell-walls cross above one another. The most important point, however, is the clearness of the preparations observed, and on these I place my dependence as to the accuracy of my statements, since there can be no doubt of my microscope being quite equal to those of foreign investigators.

I. THE PROTHALLIUM.

The specimens which I investigated were obtained from the Chelsea and Regent's Park Botanic Gardens; consisting in a great measure of self-sown plants collected from the pots of ferns growing in the stoves. Hence I am unable to give a very definite statement as to the species of ferns on which I made my observations, and can only say that they were chiefly species of *Gymnogramma*, *Adiantum*, *Pteris* and *Asplenium*; this is of the less consequence, since the phenomena appeared to differ very little in the different specimens in which specific distinctions were certainly known to exist.

Plants of *Gymnogramma chrysophylla* and of an unknown fern were obtained in the earliest condition, for among the tufts of young *prothallia* placed beneath the simple microscope for separation, I often found the burst capsule of the parent plant, with the spores germinating within and growing out from it. Examination of these showed that the first change which occurs in the spores is the bursting of the outer tough coat and the protrusion of the delicate inner membrane as a kind of pouch, like a pollen-tube from the pollen-grain; this tubular process grows longer, and sooner or later becomes divided by a cross partition into two cells (figs. 1 & 2); this is sometimes formed near the spore; in other cases the first cell is produced into a long filament before the cross-wall is formed, and the latter then partitions off a small portion at the end. The second cell becomes

elongated in like manner and again divided, and sometimes this goes on until a row of five or six cells is formed (figs. 3 & 4): when the first cell grows out into a long filament, fewer cells are formed in the simple row. Chlorophyll granules show themselves, increasing in quantity in the newly-formed parts. The first formation of radical fibres often occurs in the earliest stages, consisting in the growth outward of the wall of one or more of the cells of the filamentous *prothallium* into a slender tube, which attains a great length, remaining narrow and uniform in diameter, and never having its cavity cut up by partitions. All the roots met with on full-grown *prothallia* exhibit the same characters; they are tubular prolongations from the inferior walls of cells of the green, vegetating, frondose expansion, and their tubular cavities are freely open into those of the cells from which they arise.

After a time the youngest cell of the growing *prothallium* becomes more expanded in the transverse diameter, and after the next transverse subdivision of the cavity we find a new mode of increase, namely, a division of the newest cell in a direction parallel to the original direction of growth; by the frequent repetition of these two modes of extension the *prothallium* gradually acquires a somewhat three-sided figure, with the angles rounded off (figs. 5, 6 & 7). When it has attained a certain size a difference begins to present itself in the degree of expansion of the new cells continually formed by subdivision; those in the middle of the front border (that directly opposite to the original point of growth) remain small and are greatly surpassed in size by those at the sides and at the two anterior angles, so that the latter advance forward as rounded lobes, leaving a notch or excavation in the middle, giving the entire *prothallium* the form which in leaves, &c. is termed obcordate (fig. 9). In the meantime great quantities of radical hairs are developed from the lower faces of the cells in the neighbourhood of the obtuse apex of the heart-shaped frond, that is, about the *posterior* part of the *prothallium*, which generally exhibits a very ill-defined margin, as the cells formed at first often decay away and disappear, leaving a ragged edge (figs. 9 & 10).

While the cordate form, which varies a good deal in different species in the lateral expansion of the two lobes, is becoming perfected, the middle and posterior region of the *prothallium*, near where the roots arise, begins to display a new mode of growth. Up to this time the entire *prothallium* consists of a single flat layer of cells, in which state the lateral lobes and the anterior border persist, but in the central and posterior part the cells now become divided by horizontal walls, so as to give the *prothallium* a thickness of two, three, or more cells in the vertical section (figs. 62 & 67). The thickened portion forms a rounded cushion-like projection from the inferior face of the *prothallium* (fig. 51), while the upper surface remains flat or is even slightly depressed in the region over the thickening.

The characters presented by the cells are as follows:—their walls are delicate and closely in apposition, so as to leave no intercellular passages between them; they are lined by a layer of mucilaginous consistence (the primordial utricle) enclosing a clear fluid filling the cavity of the cell. This substance is coagulated and contracted by acids and iodine, so as to collect all the cell-contents into an isolated mass in the centre. In the cell are also found, more or less abundant, chlorophyll globules, some imbedded in the mucilaginous

layer lining the wall, others lying in the more internal parts of the cavity (fig. 13). In some cases the chlorophyll globules are so closely packed, in isolated cells, as to acquire a parenchymatous form from mutual pressure (fig. 14). These chlorophyll globules present in a high degree those characters found in the same structures in all the higher Cryptogamous plants,—characters which appear to warrant Nägeli's view that the chlorophyll is contained in a membranous vesicle, and that these vesicles are increased in number by a process of subdivision like that of cells. I have met with appearances which I cannot explain in any other way, but shall be content with a mere indication here, to avoid digressing from the immediate subject of this Memoir. I believe that I have seen the enveloping membrane enclosing a green fluid (fig. 15); moreover, the development of two or more starch-granules inside those vesicles, so as gradually to displace the chlorophyll; but as the vesicles are only about $\frac{1}{8000}$ th or $\frac{1}{10,000}$ th of an inch in diameter, much careful examination is requisite before a safe decision can be arrived at.

In some cells I have seen a small colourless and formless accumulation of mucilage upon the side wall, among the chlorophyll globules. It is possible that this may have been a nucleus. I also found a large clear and circular vesicle in one of the cells of an old barren *prothallium*; this had all the appearance of a nucleus, excepting that it was so exceedingly transparent. In the vegetative cells generally I saw no trace of nuclei.

The cells of the older posterior part of the *prothallium* contain but little chlorophyll, and like the root-filaments, are filled with colourless, slightly granular mucilaginous fluid; and they often appear stained with brown patches, arising from the partial decay of the walls. In all cases the death of the cell-membrane is followed by a brown colouring of the dead part.

Such is the normal history of a *prothallium*, so far as its vegetation is concerned (for the reproductive structures, left out of view in the preceding description, are in part developed at a very early period). If the regular development of a leafy stem takes place, a term is naturally set to the existence of the *prothallium*, which quickly decays away as the young stem grows up. But if the *prothallium* remains barren, if none of the *archegonia* become fertilized, its vegetative existence may be continued for a long time. The lateral lobes grow much larger, their borders become curved and sinuous, or variously convoluted; new lobes sometimes grow out from the cushion-like thickening in the middle; and, finally, individual cells of the margin may grow out and repeat the mode of development exhibited by the spore-cell in the original germination, so as to produce new *prothallia* (by a process of budding), which become detached from the parent (fig. 12). The progeny of 'proliferous' *prothallia* exhibit *antheridia*, but I have never seen *archegonia* upon them. In other respects they are exact repetitions of the parent structure.

II. THE ANTHERIDIA.

The organs to which this name is applied are produced in much greater abundance than those which are indicated by the term *archegonium*, and they present themselves throughout almost every stage of the growth of the *prothallium*, in some cases from the time when it consists of a mere collection of some dozen cells, in others not until the cordate form has become evident, until the latest period; so that since they run through their

course of development in a comparatively short space of time, we have them coexistent in every condition of their development in *prothallia* which are fully formed. When *antheridia* appear on very young *prothallia*, composed of a single row of cells, or at most of a double row in the upper part, they present themselves as productions from the margins, the outer side of one of the cells giving origin to each *antheridium*. But as soon as the *prothallium* has acquired anything like a flattened form, by the transverse expansion of the anterior end, the *antheridia* are formed almost exclusively upon the inferior surface, that surface in contact with the soil upon which the plant grows. They appear first upon the older cells of the central region, and gradually spread forward as the *prothallium* grows, but appear seldom to extend beyond a certain distance from the centre, occurring in greatest number about the central cushion-like protuberance above described.

It has already been stated that they occur upon the progeny of the proliferous barren *prothallia*; in some cases I have found these branching at their edges and bearing *antheridia* in a very abnormal position, at the ends of projecting cellular processes (figs. 27-32); this, however, afforded great facility for observing the internal structure of these organs, and checking the results obtained by observations upon sections.

The first sign of the production of an *antheridium* consists in the elevation of a globular protuberance from the lower, free surface (or in the young *prothallia* from a lateral surface), forming at first a kind of globular pouch (fig. 17), in which are seen at first a few chlorophyll globules, which afterwards vanish and give place to a collection of light yellowish, mucilaginous contents, slightly granular. A septum is soon formed, shutting off this budding cell from that which gives origin to it, and as it becomes elongated another cross septum often appears, a little higher up (figs. 21 & 29, &c.), so that the structure then consists of a basal cell forming a peduncle, as it were, for the proper antheridial structure. This occurs most distinctly in marginal *antheridia* (figs. 27-32).

The antheridial structure, at first consisting of a simple cell, exhibits a considerable collection of protoplasm occupying the greater part of its cavity; but this portion soon becomes defined by a circular wall, which makes its appearance simultaneously all round the central contents, converting the simple cell into a compound organ, consisting of a central cell surrounded by an annular cell; while a horizontal septum is formed above and at right angles to this, cutting off a new cell, convex above and flat at the surface, in contact with the contents.

In *antheridia* produced on young *prothallia*, the enveloping tubular cell surrounding the central cell (the parent-cell of the *sperm-cells*) does not always undergo further subdivision, but in fully developed specimens (when the basal, peduncular cell is often absent) the tubular cell appears to be divided into two by a horizontal septum running all round. This wall is seen most clearly in old *antheridia* which have discharged their contents (figs. 48, 49).

The central cell meanwhile acquires an increased quantity of protoplasm, which also appears to become more dense; these contents by their increase cause the walls of the cell to bulge out in all directions, and at a certain stage they seem to press so much upon the inner wall of the annular cell, forming the boundary of the central cell, as to push it quite against the outer wall, in fact so as to flatten the boundary cell, and for the time to efface

its cavity. The same takes place upwards and downwards, and thus the *antheridium*, when examined in this state, seems to consist merely of one large cell (figs. 21, 22 & 26), with rather thick walls consisting of a double membrane (figs. 24, 25).

While in this expanded condition the entire structure increases in size, and the contents of the central cell become more granular. After a time faint lines can be detected running through the *protoplasm* (fig. 21), and these soon display themselves more clearly as the boundaries of square isolated masses of the protoplasm (figs. 22 & 25), the nascent *sperm-cells*. Around each of the little masses thus isolated a membrane is formed. It was impossible to ascertain whether the parent-cell was first divided into a number of square partitions, by cross walls, thus producing "special parent-cells," for the *sperm-cells*, like those formed in the development of pollen-grains, the original partitions subsequently becoming dissolved to set free the cells thus originally connected together; or, whether the protoplasm was simply entirely broken up into a number of isolated portions, each of which secreted a membrane and thus formed a free cell; but I incline to believe that the latter was the fact, and that the same occurs in the completely similar case of the production of a number of closely packed endosperm-cells, in the embryo-sac of many *Phanerogamia*, as in the *Cruciferae* and *Scrophulariaceae**. However this may be, the result is the production of a large number of free cellules, filled with mucilaginous protoplasm (figs. 26, 34), of a light yellowish colour, becoming gradually more and more granular. As these cellules, at first squarish, enlarge, they become spherical, and by their expansion distend the parent-cell and disguise the existence of the annular cell surrounding it. Their number, in well-developed *antheridia*, seems to be between thirty and forty, probably never exceeding the latter number.

The free cellules, the *sperm-cells*, become more and more opaque and granular, and after a time spiral lines may be detected in them, while still within the parent-cell in the *antheridium* (figs. 35 & 36). At this time the *antheridia* may be burst very easily by pressure (fig. 36), and the *sperm-cells* which escape can be observed in all stages of development, until a spiral fibre can be clearly seen, coiled up in the interior. Specimens lying in water, under the microscope, now frequently exhibit a movement of the contents of the *sperm-cells*, they swell up, and the spiral lines are seen to change their position. Very often the bursting of the *sperm-cells* takes place within the *antheridium*, and the *spermatozoid* becomes free (fig. 38). But usually, and apparently normally, the cellules are discharged entire from the *antheridium*. This occurs by the splitting of the line of junction of the lenticular cell crossing the *antheridium* with the lateral cell, at first at one side and then usually all round, but sometimes it remains attached by a small portion (fig. 48). By this circumscissile dehiscence the cavity of the *antheridium* is freely opened, as when the lid is removed from a box. The *sperm-cells* begin to escape as soon as the dehiscence commences, and a large portion of them have often made their exit before the lid has completely opened.

As the opening of the lid gives a vent to the contents of the distended central cell, the tubular enveloping cell exerts a pressure inwards by striving to regain its original form, and as the *sperm-cells* are discharged, the side-walls of the central cell come back into

* I have observed it in *Lathraea Squamaria* most distinctly.

their former position so as to render the existence of the enveloping cell or cells very evident. After the whole of the contents have been discharged, the walls of the parent-cell acquire a deep brown colour, presenting a peculiar appearance and making the anatomical structure of the *antheridium* very clear (figs. 48, 49). The lower faces of full-grown *prothallia* exhibit, when moderately magnified, a great number of circular bodies with brown roundish or squarish central patches; these are effete *antheridia*, with the brown walls of their cavities showing through the orifice at the summit (see figs. 19 & 50).

We have next to consider the appearance of the *spermatozoids*, produced by the *sperm-cells*. These cells, as stated already, generally emerge entire from the *antheridium*, the spiral fibre being visible, in movement, in their interior. After a variable time, according to the stage of development of the *spermatozoid*, it breaks through the wall of the *sperm-cell*, and if perfect, escapes entirely from it. When perfect it appears to consist of a flattened band, curled spirally into about three and a half coils, bearing all along the outer edge, cilia of considerable length, vibrating with great rapidity; so much so, indeed, that they appear only like a fringe of light while the *spermatozoid* is in active motion (fig. 40). The filament when in the condition of the lowest specimen in the group (fig. 40) measures about $\frac{1}{1000}$ th of an inch in length, as coiled up; the diameter of the widest coil, about equal to that of the *sperm-cell*, is usually about $\frac{1}{2000}$ th of an inch. I never saw one uncoiled and flaccid but once; this measured about $\frac{3}{2000}$ ths of an inch in length (fig. 42 a). The motion consists of a rapid rotation around its axis, which, from the spiral form, causes a motion of great velocity, forwards, in the water. The motion does not seem to follow any fixed rules; the *spermatozoids* dart here and there, turn aside or backwards, or alternately to the right and left in their course onward, so as to preclude the possibility of laying down any formula or law for it. If they come in contact by the smaller extremity with any fixed body, they often adhere by this point and then revolve around their axes without advancing. By degrees the motion becomes slackened and the rotation is lost, merely a kind of vibratory motion remains, and this at length ceases; but the *spermatozoids* seem to undergo dissolution during this time, and when they come to rest often appear as shapeless masses. By applying iodine the movement of the most active can be stopped instantaneously, and in this way a tolerably clear view of the structure is obtained. Under these circumstances the cilia may be seen pretty clearly (fig. 41); the flattened band exhibits minute granules adhering to it, and is seen to have a little rounded head, from which the coils run back, increasing successively in diameter, so as to give a conical form to the outline of the whole, as seen at the side.

Such, so far as I can make it out, is the character of a perfect *spermatozoid*. But these bodies acquire the capability of motion, of whatever nature this may be, before they are perfectly developed, and hence, I imagine, the different accounts which different observers have given of them. It seemed to me that when they had not acquired their full development, the fibres could not unroll into the true form when they emerged from the *sperm-cell*; they thus appeared to present fewer coils, often only one and a half, the latter of very large diameter; in other cases they looked like minute shells of Gasteropodous Mollusks. In fig. 46 I have given representations of several of these forms, and it should be observed that these imperfect forms exhibited a greater quantity of adherent granules, and

a less definite outline than the others. Finally, some appeared unable to extricate themselves from the sperm-cell, and carried this along attached to the posterior extremity (fig. 44). This vesicle attached to the *spermatozoid* has been described by some observers as formed by the swelling of the extremity of the filament after its exit from the sperm-cells, therefore as constituting an integral part of the structure of the *spermatozoid*; but I believe this to be an error.

In one case I saw an appearance which seemed to indicate the existence of a hair-like production of the posterior extremity of the *spermatozoid*, like that figured by Hofmeister. A *spermatozoid* moving rapidly forwards in the water dragged after it, at a little distance, a small mass of mucilage (fig. 42 *b*); the bond of connection was invisible, and therefore, most probably, must have consisted of a capillary process. I never saw any hair-like tail in specimens suddenly paralysed by iodine, but it may have escaped notice from its tenuity; on the other hand, it may possibly be only found in the most perfect state of the *spermatozoid*, and since these are examined under artificial conditions, often causing the rupture of the *antheridia* before their contents are mature, the most perfect condition may only be met with occasionally.

III. THE ARCHEGONIUM.

In the description of the development of the *prothallium*, it has been stated that a thickened, cushion-like mass is formed in the central region, by the time the general form has become complete (fig. 51). This central mass is composed of several layers of cells, and, projecting from the general surface, does not reach quite to the inner extremity of the anterior notch of the *prothallium*, so that an inclined surface is produced looking somewhat forwards toward the notch (fig. 52).. Upon this arise the *archegonia*, which are variable in number, seldom however exceeding six or eight.

The earliest rudiment of the *archegonium* is the *embryo-sac*, as it may be termed, consisting of one of the cells of the thickened cushion, separated by a single cell from the (inferior) surface of the *prothallium* (figs. 54—57 *a*). A cell, destined to become an *embryo-sac*, is found surrounded by a circle of cells of smaller size than those of the surrounding tissue, and formed by the production of walls in the cells immediately bordering the *embryo-sac*, tangential to the circumference of the latter, which thus becomes defined by a wall of small cells surrounding it (figs. 55, 57 *b*). Cell-division also takes place in the cells beneath the *embryo-sac*, and these multiply so as to form a collection of condensed tissue enclosing the *embryo-sac* at the sides and below (figs. 66, 67 *b*), visible through the cells of the surface of the *prothallium* (figs. 54, 56) before the external structure is formed. The commencement of the development of this consists in the enlargement of the cell separating the *embryo-sac* from the surface, and its division into two cells by an inclined wall, the larger of these being again divided by another partition at right angles to the former, so that as seen from the (under) face of the *prothallium* (fig. 52), the superficial cell seems divided into three. I could not follow the development of the cells, step by step, onward from this point, but it is evident that they go on repeating the mode of subdivision of the first cell; that is to say, the process is as follows: the original cell, *A*, divides by an oblique septum into an upper, *b*, and lower, *a*, the latter being divided by a radial septum into

two, *a* 1, *a* 2; the cell *b* expands upwards, and by the formation of a septum inclined exactly in the opposite way towards the horizon, to that first formed, cuts off cell *b* into *b* and *c*; *b* is then divided by a radial septum into *b* 1 and *b* 2, while *c*, the last new cell, overlaps *a* 1 and *a* 2; another division of *c* leaves *c* 1 and *c* 2 over *a* 1 and *a* 2, and carries up *d* to form *d* 1 and *d* 2, above *b* 1 and *b* 2, until the papilla reaches its full height, and appears composed of tiers of four quadrant-shaped cells, the first tier consisting of *a* 1 and *a* 2, *b* 1 and *b* 2 of the series; the next tier of *c* 1 and *c* 2, *d* 1 and *d* 2, &c. (figs. 58–61).

In the meantime, the *embryo-sac* at the base, which very early appeared filled with opakish protoplasm, comes to exhibit a central globular body (figs. 56, 57 *c*), which in all probability is an isolated mass of protoplasm, destined to secrete a membrane around it, and to form the *germinal vesicle*, just as occurs in the embryo-sac of Phanerogamia (for example in *Orchis*). The next peculiarity is the appearance of a clavate cavity running up the centre, between the convergent inner angles of the four series of cells of the papilla, forming a canal evidently communicating, through a constricted neck, with the *embryo-sac* (figs. 62–70). In this canal is observed a slender clavate filament of slightly granular muelage (fig. 70) running down into a point in the *embryo-sac* below, where I believe it is in contact with the *germinal vesicle*: I imagine this to be a portion of the protoplasm of the *embryo-sac* which has been protruded up into the intercellular canal of the papilla, after the absorption of the wall of the *embryo-sac*, where it at first closed the bottom of the canal at the constricted neck. After a time the canal becomes opened to the external medium, and then the clavate filament is often seen hanging out from the open mouth (figs. 63–66); it is generally double (figs. 63, 64) at the upper end, which I cannot explain. It appeared firmly attached in the canal, and bore the movements of the preparation, by pressing and sliding over the covering glass, without becoming detached from the papilla.

It is at this stage of development that I believe the impregnation to take place; but before proceeding to speak of this part of the subject, I may conclude the description of the *archegonia*, by stating that the greater part of them are abortive; very rarely more than one being fertilized on a *prothallium*, and very often none. When thus abortive the cellular papillæ continue growing to some extent, the central canal becomes widely opened, often into a large funnel-shaped orifice, and the walls of the intercellular canal and the *embryo-sac* acquire the same deep brown colour as the interior of the effete *antheridia* (figs. 72–74).

IV. DEVELOPMENT OF THE EMBRYO.

My opinion with regard to the fertilization is, that the operation is effected by the contact of one or more *spermatozoids* with the mucilaginous filament contained in or hanging from the mouth of the canal of the *archegonium*. I have seen the *spermatozoids* swimming in numbers around the mouth of the *archegonia*, but never detected one inside, and I do not see any good reason for supposing such a process necessary. The pollen-tube of flowering plants only comes in contact with the outside of the embryo-sac, and the influence is sometimes communicated through a long suspensor; and there does not seem to be any sufficient objection to the supposition, that the contact of the *spermatozoid* with the filament of muelage which lies in the canal of the *archegonium*, suffices to convey the

necessary stimulus. I imagine this stimulus resides in the mucilaginous fluid in which the *spermatozoid* is bathed in the *sperm-cell*, and which, adhering to this, is conveyed to the mucilage (protoplasm) of the *germinal vesicle*, just as the contents of the pollen-grain become combined with the protoplasm of the germinal vesicle in flowering plants. The nature of the process is clearly a problem beyond the reach of science, but it seems to be a necessary induction, from the facts in the Phanerogamia, that the phenomena result there from the material union of two fluids, and I hence conclude that this is the case here. The comparatively few cases of successful impregnation among these *prothallia*, so many of which prove sterile, may perhaps be accounted for by the peculiar conjunction of circumstances required to bring a sufficient amount of the fertilizing fluid, by means of the *spermatozoids*, to the *germinal vesicle*, at the precise epoch required.

Some doubt has been thrown upon the possibility of the impregnation of the *archegonia* by means of the *spermatozoids*, on the ground that the free movement of the latter in the water, beneath the microscope, is an abnormal condition. I attach no weight to these objections, for the occurrence of numerous empty *antheridia*, on moderately developed *prothallia*, proves that their dehiscence is a natural process, and if the moisture which always exists upon the under surface of the *prothallia* is insufficient to allow such a wide and free course to the *spermatozoids* as they find in the water on the glass slider beneath the microscope, we see a compensation for the obstacles in the way of the conjunction in the large number of *antheridia* produced, and this not at one time only, but throughout the whole growth of the *prothallium*. Again, there is evidence that the process is not easily and constantly completed, in the fact of so many *prothallia* remaining sterile, and in the provision of several *archegonia* upon each, while in normal cases only one produces an embryo.

Arguments have been urged against the entrance of the *spermatozoids* into the *archegonium*, from the consideration that the mouth of the canal is directed downwards, and the *spermatozoid* would consequently have to work its way upwards, contrary to the attraction of gravity; and further, from the fact that the apex of the *archegonium* is usually directed forwards towards the notch of the *prothallium*, while the *antheridia* occur principally about the posterior part. If we imagine the contact of the *spermatozoids* with the mucilaginous matter protruding from the mouth of the canal to suffice for the impregnation (it being understood, however, that this happens under such circumstances that the *spermatozoid* is fresh from the *antheridium*, and the mucilage of the canal of the *archegonium* has not yet become coagulated by exposure), this difficulty is done away.

The first result of the impregnation,—that is to say, the first step of development of the embryo, which I believe to be the consequence of such an operation,—as seen by means of vertical sections of the *prothallium*, consists of subdivision of the *germinal* or *embryonal vesicle** of the *archegonium*. In the earliest state that I have been able to see clearly, a little globe of minute cellular structure occupied the place of the *embryonal vesicle* (figs. 71, 75),

* It is unimportant which we call it, since it is here developed at once into the embryo. In flowering plants the *germinal vesicle* usually becomes subdivided to form a suspensor, and one of the cells produced by it becomes the *embryonal vesicle*.

in the *embryo-sac*. The succeeding stages of growth of this new cellular body, the *embryo*, consist of a gradual multiplication of the cells by division, and expansion of the new structure, until at length the rudiments of a radicle and the first leaf become visible as projections from the surface, resulting from the more rapid increase of the cells in the situation where they are found (figs. 76-79).

In the ulterior development of the *embryo* the radicle appears to be arrested in its development, and to remain as a cellular mass (fig. 80 *a*) within the cavity of the *prothallium*, until it disappears with the latter by decay. The first leaf unfolds upwards and forwards (fig. 80 *b*) towards the notch of the *prothallium*, and the first adventitious root (fig. 80 *c*) breaks through at the base of this towards the posterior border of the *prothallium*, exhibiting a coleorhize like that of the Monocotyledons. The second leaf arises near the axil of the first, one-third of the circumference of the nascent stem to the side; the third leaf arises one-third to the side of the second, so that the three leaves form a circle, in which they stand at equal distances, and the fourth leaf arises over the first (*Gymnogramma chrysophylla*?). They are of very simple structure, consisting of cellular plates with twice-forked rudimentary nervures, and they are accompanied by very elegant *ramenta* at the bases of the little petioles (figs. 81-83).

I have not followed the development beyond the formation of the fourth leaf (fig. 83), by which epoch the *prothallium* has generally decayed away from the base of the young stem.

V. CRITICISM OF PREVIOUS OBSERVATIONS.

The first account of any of the peculiar structures above described was published in 1844 by Nägeli*, in a memoir entitled "Moving Spiral Filaments (spermatic filaments) in Ferns," wherein he announced the existence of the bodies now called *antheridia*, but mistaking the *archegonia* for modified forms of the *antheridia*, he was led away from a minute investigation of them. If he had followed the development of the *prothallia* further, he would have detected the relations of the nascent embryo, which would probably have put him on the right track. As it was, the remarkable discovery of the moving spiral filaments, or *spermatozoids*, occupied all his attention, and caused him to fall into error in certain important respects; for example, in fig. 11 of his plate, he has represented what is undoubtedly an *archegonium*, filled with cellules (*sperm-cells*), which, he states, emerged from it as from the *antheridia*: this is undoubtedly incorrect.

With regard to the *spermatozoids* his description is imperfect, the only indication of the existence of cilia being a statement that he occasionally saw a long filiform appendage, like that represented by Meyen in the *spermatozoids* of *Chara*. On the other hand, the mathematical definition of the movements of the *spermatozoids* is surely misplaced, since nothing can be more arbitrary or irregular than their course.

However, whatever be the faults of observation, it is certain that it is to the keenly inquiring spirit of this author that we owe the first step of the investigations which have thrown so much light upon the reproduction of the higher Cryptogamia.

Nägeli's observations remained without confirmation or criticism until the publication

* Zeitschrift für wiss. Botanik. Heft i. 168. Zürich, 1844.

of the important investigations of Count Suminski, which were first made known in the 'Bulletin' of the Berlin Academy, and by a note from Dr. J. Münter in the 'Botanische Zeitung,' but were given in a complete form in a separate treatise by the author in 1848*.

These investigations, which form the basis of the subject before us, from the capital fact of the discovery of the *archegonia* and of the development of the embryo from one of these, present a curious mixture of industrious observation and preconceived theories. It is an invidious task to criticise an essay which has so greatly advanced our knowledge of the subject, but it is an unavoidable one. The great fault of the essay is the free exercise of the imagination in cases where the delicacy of the structures renders the objects exceedingly difficult to make out clearly. I feel warranted in making this assertion by the fact that my own microscope must be equal if not superior to that used by Count Suminski, since I have seen, with the greatest clearness, points which he missed, where good definition of the microscope was all that was requisite, and on the other hand, I can trace actual invention in cases where bad definition of the object would leave points obscure which I saw distinctly. Moreover, his figures display appearances which I neither saw nor can conceive the possibility of seeing with the distinctness represented in his drawings, while some of these bear patent evidence of a faulty interpretation of tolerably clear conditions.

Such assertions of course require evidence, and it is desirable that this should not rest upon counter-statements alone, but should furnish some explanation of the probable causes of the errors stated to exist.

In the first place, then, Suminski describes the growth of the cells of the *prothallium* to take place by the formation of two or more free cells within a parent-cell, expanding till they come in contact, and meanwhile displacing the chlorophyll and other contents of the parent-cell, which become absorbed and are reproduced in the new cells. This statement is opposed to all my experience of vegetative growth, not only in these *prothallia*, but in all other plants; and is evidently a hasty conclusion, arising out of a preconceived notion,—that notion of cell-formation formerly asserted by Schleiden to be universal, but now acknowledged by him to be subject to exception: for I can affirm that the growth of the *prothallium* occurs by the expansion and subdivision by septa of the cells, without important disturbance of the contents, and this process is in all probability effected through the agency of the *primordial utricle*, or layer of dense protoplasm which invariably lines the walls of the growing cells.

With regard to the *antheridia*, Suminski observed them very superficially; he describes the compound cellular body borne upon a peduncular cell, as a simple cell, discharging the *sperm-cells* by bursting. He overlooked therefore all the stages of development, from the very earliest up to the time just preceding the dehiscence, and can scarcely have paid any attention to the appearances of the effete *antheridia*. I need only refer to the observations of Thuret, Schacht and Hofmeister to prove how imperfect his account of the *antheridia* is. The *spermatozoids* inside the *antheridia*, again, and those in the free

* Zur Entwicklungsgeschichte der Farrenkräuter, von J. Grafen Leszezye-Suminski. 4to, Berlin, 1848.

cellules, shown in Suminski's figures (pl. 2. figs. 12-16), are, like those of the *antheridia*, derived rather from the imagination than from fact.

But the most important errors occur in the account of the development of the *archegonia*. The earliest stage, as seen by looking directly upon the (under) surface of the *prothallium*, was completely misconceived by Suminski. He overlooked the cell, forming part of the general surface of the *prothallium* and becoming the parent-cell of the papilla, which, from the first, lies between the *embryo-sac* and the external medium; so that he imagined the *embryo-sac* to be open and capable of admitting *spermatozoids* into its cavity. I examined this point most carefully, and am convinced that he was in error. Any one who looks at his figs. 1 and 2 of plate 3. will see that there exists no trace in them of a cell or cells from which the papilla (seen from above in fig. 3 of his 3rd plate) could arise, for the supposed orifice is bounded by seven cells, and if the papilla sprang from these it would consist of seven vertical series instead of four. The fact is, that his fig. 1 of pl. 3, stated to be from a dissection, merely shows what is seen in looking upon the under surface of the *prothallium*, without dissection; but it represents the object focused down to the globule in the *embryo-sac*, as in my fig. 57, so that the membranes of the cells occupying the space supposed to be an orifice and forming part of the continuous surface of the *prothallium* (my fig. 56) are not seen. Fig. 3 of Suminski's 3rd plate shows a subsequent stage, where the papilla, composed of four rows of cells, is already developed; he has missed the gradual production of this from the cell occupying the situation of the imaginary orifice.

This clearly takes away all ground from his hypothesis of the impregnation resulting from the entrance of *spermatozoids* into the *embryo-sac* before the development of the papilla of the *archegonium*, and moreover proves that the bodies contained in the closed canal of this organ (shown in his figures, pl. 3. figs. 4-7) could not be altered *spermatozoids*. It will be remembered that I have explained these appearances in a totally different way.

With regard to the phenomena of the development of the *germinal vesicle* in the *embryo-sac*, I think it is scarcely possible to obtain such clear views of the young structures as Suminski has given, and I could only approximate to them by sections through the *prothallia*, while from his figures we are led to suppose that he saw them through the enveloping tissues, which are far too thick to allow such clear definition, especially since their contents soon become coagulated by the injury the preparation suffers in water and under pressure. All that Suminski states, therefore, respecting the development of a cellule at the end of the *spermatozoid*, inside the globular cell of the *embryo-sac*, I regard as the work of imagination, guided by a preconception of the necessity of some process analogous to that described by Schleiden in reference to flowering plants, namely, the production of the embryo from a cellule formed in the end of a pollen-tube, after the latter has become imbedded in the embryo-sac. The drawings representing the subsequent growth of the *embryo* are more or less incorrect; thus the primary, undeveloped radicle, which remains enveloped in the tissue of the *prothallium*, is not properly shown, while this cellular tissue is represented as enveloping the base of the leaf and of the first adventitious root (pl. 4. fig. 10 *f.* of Suminski's Essay), and the adventitious root itself as a direct prolongation from the base of the first leaf. The true condition is shown in my

fig. 80, where the ragged tissue (*h*) is seen to be the torn edge or collar always found where adventitious roots break out from the interior of a stem.

It is unnecessary to enter into any other points. It is seen that the only matter in which I am agreed with Suminski is the import of the organs and the existence of a sexual conjunction; in all the details of the processes I am at variance with him. Nothing, however, can take from him the credit of having discovered the *archegonia* and their import, one of the most important discoveries in physiological botany of modern times; since it has led to results revolutionizing the whole theory of the reproduction of plants, and opened out a totally new sphere of inquiry into the laws and relations of vegetable life.

The next contribution to the subject to which such a lively interest had been attracted, was a paper by Dr. Wigand*, giving a detailed account of a series of critical observations on the question, and deducing conclusions directly opposed to those of Suminski. Dr. Wigand's observations do not seem to have been complete and thorough-going, for he also describes the perfect *antheridium* as a single cell, and appears to have confounded the complex structure seen in the effete *antheridia* with that of the *archegonia* (p. 23 *loc. cit.*). His description of the development of the sperm-cells within the *antheridia* is nearer the truth; but while right in rejecting the ideas of Nägeli and Suminski, that these originate by free cell-formation around a nucleus, he fell into a different error in supposing that the cellules were not in contact at first, but were formed in groups around isolated portions of the cell-contents. His description of the *spermatozoids* is pretty accurate, but the differences he describes appear to me to indicate different stages of development, and not to depend upon the specific differences of the specimens examined. He overlooked the earliest stages of the growth of the *archegonium*, and especially the existence of the *embryo-sac* beneath the nascent papilla; the account of the later stages of development of the papilla is tolerably correct. But he observed the later conditions of the abortive embryo-sacs separately, and as independent organs, which he called "peculiar glandular structures" (p. 49 *loc. cit.*), and he argued directly against their being considered as connected with the papilliform structure, closed at its summit, forming the upper free portion of the *archegonium*.

Dr. Wigand contends at great length against the existence of a process of impregnation, but the only fact of importance I find in his arguments is the statement that he found buds (*embryos*) in many cases where no *archegonium* existed on the *prothallia*. This is contrary to my experience, and I feel confident that his investigations were imperfect in this respect. Many pages of *arguments* which he urges against Suminski's views may be passed over, since my own observations, if, as I fully believe them, correct, remove the necessity for discussion, by showing the *facts* to be different. With regard to Dr. Wigand's arguments against the probabilities of the fertilization, I think it unnecessary to enter into them, as the analogous conditions since discovered in the allied groups of the Cryptogamia, especially those recently demonstrated to exist in the Lycopodiaceæ and Rhizocarpeæ, turn the balance of probabilities the other way.

* Zur Entwicklungsgeschichte der Farrenkräuter, von Dr. Albert Wigand. Botanische Zeitung, vol. vii. p. 17 *et seq.* 1849.

Lastly, it is unnecessary to criticise Dr. Wigand's views as to the origin of the *embryo*, or, as he calls it, the "bud" of the new plant, since he admits that he did not trace the earlier stages of its development, and seems never to have investigated it by sections, so as to see the relations with the embryo-sac. His *opinion* was that no relations did exist.

Shortly after the appearance of Dr. Wigand's memoir, M. G. Thuret* published an account of the *antheridia* and their contents, the particulars of which agree pretty closely with those I have given. He states the structure of the *antheridium* to be less simple than Suminski and Wigand had described it, consisting of a parent-cell of the *sperm-cells* surrounded by an annular cell, but not by a collection of flattened cells such as Schacht and Hofmeister describe. He does not enter minutely into the development of the *spermatozoids*, but describes them accurately, excepting, as I believe, in reference to the hyaline vesicle, which he says they *ordinarily* drag about with them; this vesicle, which in a later paper† he states to be in all probability a product of the *spermatozoid*, I consider to be the parent *sperm-cell*, from which the *spermatozoid* has not completely extricated itself, and I did not find it in the majority of cases.

In the same year M. Hofmeister published a brief preliminary summary of his observations on the reproduction of the Cryptogamia‡, wherein he arrived at conclusions which approximate pretty closely to those I have given, but to which I shall refer more particularly presently, in analysing the portion referring to the Ferns of his great work on this subject.

The next important contribution was an elaborate paper by M. Schacht§. In examining this it is unnecessary to repeat the particulars in which he agrees with all other authors, and I shall therefore confine myself to the debated points.

In reference to the *antheridia*, where he differs from Thuret and myself, he states that the envelope of the parent-cell of the *sperm-cells* is composed of a number of cells, the annular cell which I have described being supposed to be divided by four perpendicular walls, so as to form four cells constituting a quadrangular boundary to the central cell. Where a horizontal septum exists, the envelope would consist of eight cells forming two circles of four. This view I hold to be incorrect, for I never could see the numerous boundary lines which such a structure would exhibit, in the hundreds of *antheridia* which I have examined. He also supposes that the *sperm-cells* originate by free cell-formation in the central cell, which I must distinctly deny.

Schacht describes the *spermatozoids* as having four and a half or five turns in the spiral coil; I believe three to four is the utmost: moreover, he regards the widest convolution as the anterior, a view which I cannot explain, and he states that this passes into a vesicular structure which swells up in water (as described by Thuret); this I consider the *sperm-cell*, still adherent to the *spermatozoid*.

* Note sur les Anthéridies des Fougères, par G. Thuret, Ann. des Sc. Nat., 3rd Ser., Botanique, t. xi. p. 5.

† Ann. des Sc. Nat., 3rd Ser., Botanique, t. xvi. p. 29, 1851.

‡ Ueber die Fruchtbildung und Keimung der höheren Kryptogamen. Botanische Zeitung, vol. vii. p. 793, 1849.

§ Beiträge zur Entwicklungsgeschichte der Farrenkräuter, von Hermann Schacht. Schlechtendahl's Linnæa, xxii. p. 753, 1849.

The *archegonia* are stated by him to be found exclusively upon the thickened part of the *prothallium* (in opposition to Wigand), as I have described them. He further says that the earlier stages of development are difficult to make out, but he believes the papilla originates by the subdivision of one of the cells of the *prothallium* into four by vertical septa crossing each other, these growing out into a conical body; the canal, and the cavity at the base (the *embryo-sac*) are supposed to originate as intercellular cavities, by the separation of the cells bordering them. The canal is closed at first and open afterwards. It is evident from these statements that the earlier conditions of the *embryo-sac* were overlooked. The mucilaginous filaments in the canal of the *archegonium* were seen and figured by Schacht, who correctly asserts that they are not decaying *spermatozoids*, as supposed by Suminski. He states that the embryo originates in the cavity at the base of the *archegonium* (the *embryo-sac*); but he seems to suppose it to be merely a vegetative growth, as is evident from the concluding paragraph of his memoir:—

“Since the ‘germ-organ’ (*archegonium*) is not open originally, but closed, the fact of its opening subsequently, when it has become surrounded by a high cellular wall, together with the circumstance that the direction of the orifice is downwards, render it scarcely conceivable how ‘spiral-filaments’ could make their way into it; moreover, in spite of the utmost patience and care, I could never observe a ‘spiral-filament’ inside the ‘germ-organ,’ still less the conversion of one of them into the ‘germ’ (*embryo*). Consequently the impregnation of the Ferns, as described by Count Leszczyc-Suminski, is more than improbable, and thus the inclusion of the Ferns among the *Phanerogamia* is by no means justified.”

In these conclusions we see that the bias given by the adherence to Schleiden’s doctrine of the origin of the embryo in the *Phanerogamia*, of which Schacht is one of the leading defenders, has prevented his entertaining the idea of the *spermatozoids* exerting simply a fertilizing influence. All his argument is against the conversion of one of them into an *embryo*, so that the hypothesis I have adopted is not touched by the above statement, and it is unnecessary to add further remarks.

In the following year M. Mettenius* published some important researches on this and allied points in the reproduction of the Cryptogamia, in which, however, he confined himself, in regard to the Ferns, to a description of the development of the *archegonia*. In this his statements agree in the essential particulars with those I have given above, since he also believes Suminski to have overlooked the superficial cell covering the *embryo-sac*, and giving origin by its division to the papilla which subsequently grows up. There is only one anatomical point in which I think he was probably in error, namely, in reference to the mode of development of the papilla, the projecting portion of the *archegonium*. He states that the first cell is divided into four by crossing vertical walls, that these four cells grow up equably and become divided by horizontal septa so as to form four parallel columns each composed of four or five cells one above the other, between the contiguous internal angles of which the canal leading down to the *embryo-sac* is formed as an intercellular passage. My observations, as already stated, lead me to believe that the process is somewhat different from this, and that Hofmeister’s description is more correct.

* Beiträge zur Botanik, Heft i. Heidelberg, 1850.

In the same year appeared an essay on this subject by Dr. Von Mercklin*, which I have not seen, but I am able to state the principal points in it, from the circumstance of his having published an abstract of them in the 'Linnæa†,' in answer to Schacht's criticism of Suminski's views.

Von Mercklin states that the *antheridia* appeared to him to consist of never more than five cells; sometimes they appeared still more simple, but he gives no details in his abstract. Of the *spermatozoids* he says that the figures given by Thuret and Wigand agree best with his observations, those of Suminski worst, but he regards the large vesicle figured by Schacht at the extremity of the widest coil, as the adherent *sperm-cell*. He also considers the broad convolution to be the posterior, since the *spermatozoid* always advances with the narrow end foremost; in this his statements accord with my own observations.

In reference to the *archegonia*, he truly says that Schacht overlooked the earliest stages, and he asserts that although he is not positive concerning all cases, he has distinctly seen an orifice into the cavity of the *archegonium* (the intercellular cavity, as he and Schacht consider it, but the *embryo-sac* of my description) in the situation of the cell from which the papilla grows up, pretty much therefore what Suminski described. Moreover, he states that he has seen *spermatozoids* enter this. But he does not appear to attribute importance to any particular epoch for the contact of the *spermatozoid* with the *embryonal vesicle*, which lies in the cavity (*embryo-sac*), for he states that of the three times he witnessed this phenomenon, in the course of an entire year's observation of the subject, the *spermatozoids* twice entered the nascent organ, as described by Suminski, and in the other case entered the open canal of a fully developed *archegonium*, to reach the "germ-cell" (*embryonal vesicle*). He states his belief that the mucilaginous filaments seen by Schacht, Mettenius, &c., in the canal, are really altered *spermatozoids*, and he concludes with the following assumptions:—

"1. The *spermatozoids* do regularly enter into the *archegonia*; and, 2. Probably contribute to the origin or the development of the first 'germ-frond.' How this takes place I know not, and the details concerning it, given by Count Suminski, remain for the present unconfirmed."

The last observations to which I have to refer are those contained in M. W. Hofmeister's recent work‡, forming part of an elaborate series of investigations on the reproduction of the higher Cryptogamous plants.

This author, like Schacht, describes the *antheridium* as a more complex structure than I and Thuret imagine it to be, since he believes the walls enveloping the central parent-cell of the *sperm-cells* to consist of four or eight cells, constituting a quadrangular boundary, instead of being simply one or two annular cells. He further states that he found, on young *prothallia* produced by budding from old barren and proliferous *prothallia*, *antheridia* of the

* Beobachtungen an dem Prothallium der Farrenkräuter, von Dr. C. E. von Mercklin. St. Petersburg, 1850.

† Zu den Untersuchungen über die Entwicklungsgeschichte der Farrenkräuter, von Dr. C. E. von Mercklin. Schlechtendal's Linnæa, xxiii. 723. 1850.

‡ Vergleichende Untersuchungen der Keimung, Entfaltung und Fruchtbildung höherer Kryptogamen, &c. 4to. Leipzig, 1851.

simple structure described by Suminski and Wigand, consisting of a simple cell; this statement is quite contrary to my observations; I frequently examined *antheridia* in all stages in such *prothallia*, and they differed from the normal form only, in certain cases, by being supported on elongated pedicels produced by an unusual growth of their basal cells (fig. 50). With regard to the mode of development of the *sperm-cells*, Hofmeister describes, as I have done, the gradual subdivision of the mucilaginous contents of the parent-cell into numerous cubical portions, each of which becomes clothed with a membrane and produces a *spermatozoid* within it. His description of the *spermatozooids* differs but little from mine; he asserts, however, the regular existence of a long and very slender hair-like process at the hinder extremity, which I have only seen an indication of in one case.

In his account of the development of the *archegonium* he differs considerably both from Mettenius and myself, although the final results are the same. According to him, the papillar process is formed before the basal cavity (the *embryo-sac*), by the growth outwards and subdivision of one of the superficial cells of the cushion-like thickening of the *prothallium*. He describes the formation of the *archegonium* in the following manner: the superficial cell which gives origin to it becomes divided by an oblique wall into an upper and a lower cell, the upper and larger is again divided by an oblique wall inclined in the opposite direction, and this is repeated five or six times; this would result in the formation of a papilla composed of two parallel rows of cells slightly overlapping alternately as they rise; but as they are developed each is divided into two by a perpendicular radial wall, so that the papilla consists of four conjoined vertical piles of cells. In the next place, either all or only the lowest of the cells of one of the vertical rows become divided into two by a tangential wall; so that, in the first case, a central row of cells is formed, running up the centre, or, in the second case, the extra cell is only formed at the bottom. This lowest cell, which is the *embryo-sac*, becomes enlarged rapidly; the cells of the *prothallium* immediately surrounding it become divided by septa so as to form a kind of epithelial layer around it. During this growth the canal is formed up the centre of the papilla, when the fifth row of cells exists by the solution of all but the bottom one, and when this extra cell is formed only at the bottom, by the separation of the contiguous inner angles of the four rows, so as to form an intercellular passage. The greater part of the *archegonia* undergo no further development after this canal opens at the apex, but the membrane bounding the canal and the cavity formed by the basal cell become coloured rich brown.

With regard to this description of the development of the *archegonium*, I believe it to be correct so far as relates to the production of the upper part, namely the papilla, excepting in respect to the formation of the fifth row of cells, subsequently dissolved to leave the canal open. But the mode of origin of the basal cell or *embryo-sac* is certainly contrary to my observations, since I found it before the papilla had begun to be developed, and surrounded at this early epoch by the so-called 'epithelial' layer (figs. 54-57), the papilla being produced by the cell lying outside it.

Hofmeister declares in favour of the entrance of a *spermatozoid* into the canal of the *archegonium*, to fertilize a little spherical cell (the *embryonal vesicle*) originating in the basal cell or *embryo-sac* of the *archegonium*; this cellule then begins to expand and to be

subdivided, so as to form a globular mass of cells, in which the prominences indicating the radicle and leaf soon make their appearance.

He never saw the actual entrance of the *spermatozoid* into the *archegonium*.

VI. CONCLUSIONS.

In summing up all these statements it becomes evident that the balance of evidence is in favour of the existence of sexual organs, and of a process of impregnation, giving rise to a new individual, as asserted by Suminski, although under conditions somewhat different from those described by that author. Only two of the observers who have repeated his investigations throw doubt upon these points, namely Wigand and Schacht: the statements of the former as to matters of fact are far from sufficient to bear out the mass of argument he has built upon them against the existence of sexes; in fact, his observations were so imperfect, that he described the two parts of the *archegonium*, the *papilla* and the enlarged *embryo-sac*, as distinct structures, while he never traced the origin of the new plant at all. His observations may therefore be safely passed over. Schacht's are more complete, but he again only *argues* against the probability of a sexual conjunction, with the preconceived notion that this must be analogous to what he erroneously believes to be the conditions in the Phanerogamia; while his observations furnish facts which greatly support the probability of an impregnation by the *spermatozoids*; the difficulties he suggests being of little weight in comparison with those of accounting for the existence of all the peculiar structures by any other hypothesis.

The opinions of all the rest are in favour of the impregnation (Thuret does not treat of the *archegonia*); and the differences between them, except in the case of Suminski, are unimportant in a physiological point of view, merely presenting questions of anatomical and morphological interest. And since Suminski's description of the mode of origin of the embryo would be altogether at variance with what exists, not only in other plants, but also in animals, and is opposed to the observations of all the rest of us (except the doubtful support given by Von Mercklin), I cannot but repeat my belief that he was led away from the facts by his imagination being preoccupied by Schleiden's doctrine of the impregnation of the Phanerogamia.

These observations on the Ferns have acquired vastly increased interest from the subsequent investigations of Hofmeister, Mettenius and Nägeli on the allied Cryptogams, and above all, from Hofmeister's observations on the processes occurring in the impregnation of the Coniferæ*.

Not only have these investigations given us a satisfactory interpretation of the *archegonia* and *antheridia* of the Mosses and Liverworts, but they have made known and coordinated the existence of analogous phenomena in the Equisetaceæ, Lycopodiaceæ and Rhizocarpeæ, and shown, moreover, that the bodies described by Mr. Brown in the Conifers, under the name of 'corpuscles,' are analogous to the *archegonia* of the Cryptogams, so that a link is hereby formed between these groups and the higher flowering plants.

* Vergleichende Untersuchungen, *loc. cit.*

It would be out of place to enter into a detailed examination of these discoveries at the close of this long memoir. They are to be found in the work of Hofmeister* already quoted in regard to the Ferns. I may also refer to a *resumé* of the present state of knowledge on these subjects, published by myself in the 'Annals of Natural History †,' for the facts and general conclusions to be derived from them, and to a Report furnished to the British Association in 1851, for an account of the historical development of these questions during late years.

I cannot conclude without once more directing attention to the many striking analogies recently revealed between the phenomena of reproduction in plants and in animals. They must excite the strongest interest in the minds of all those pursuing the study of biological laws. Many of the facts rest, at present, it is true, upon the authority of but one or two observers, and it can scarcely be doubted that much remains to be discovered before all the details are sufficiently established. The investigation of the reproduction of Ferns is the point which has been most pursued hitherto, and even here there is considerable discrepancy in reference to anatomical conditions. My own observations have satisfied me only after prolonged and careful study of the subject; for where we have to compare successive stages in distinct preparations, and this by means of dissection of microscopic structure, there are very numerous inlets for misconceptions. If I have fallen into errors, I trust they may be soon detected by other observers, whom this memoir may attract to similar researches.

London, May 1852.

DESCRIPTION OF THE PLATES.

TAB. XIV.

[The specimens were in most cases self-sown plants, and moreover were often mingled before examination, so that I am unable to say more than that they belonged principally to an unknown *Adiantum*, an *Asplenium*, *Pteris serrulata*, and *Gymnogramma chrysophylla*. Most of the stages, however, were observed repeatedly in the last species. The drawings were all made in outline with the aid of the camera lucida eye-piece, except in the cases of Figs. 33, 41-47, and 75.]

Figs. 1 & 2. Germinating spores: the second figure exhibits a radical filament.

Figs. 3 & 4. More advanced specimens.

Figs. 5-8. Subsequent stages, in which lateral expansion is going on.

Fig. 9. A young *prothallium*, in which the peculiar obcordate form is already distinguishable.

Fig. 10. Under surface of a young *prothallium* of tolerably complete form, before the thickened cushion has made its appearance in the middle.

Fig. 11. A more highly magnified view of half such a *prothallium*, in which a number of *antheridia* exist (under surface).

Fig. 12. A young *prothallium*, produced by budding from the margin of an old sterile (proliferous) *prothallium* (under surface).

* See *ante*, page 133.

† June 1852.

- Fig. 13. Greatly enlarged view of two cells of a *prothallium*, showing the position and appearance of the green chlorophyll globules.
- Fig. 14. Another cell, occurring isolated among others of the ordinary character, in which the large chlorophyll globules have acquired a parenchymatous appearance from mutual pressure.
- Fig. 15. Chlorophyll globules very much magnified, exhibiting (starch) granules within, and apparently a membranous coat.
- Fig. 16. Magnified fragment of a *prothallium* from the neighbourhood of the anterior notch (under surface), bearing several *antheridia*, some imperfect, one ripe, two effete: the lowest is seen sideways, and the structure is made evident by the brown colour of the membrane of the cavity which has discharged its *spermatozoids*.
- Fig. 17. Two cells, from which *antheridia* are being formed, by budding out from the lower faces; the left-hand one is the youngest and contains a little chlorophyll; in the right-hand one the chlorophyll has given place to dense protoplasm.
- Fig. 18. Marginal *antheridia*, almost ripe.

TAB. XV.

- Fig. 19. *Antheridia* in various stages; the brown one has discharged its *spermatozoids*. *a.* represents a brown peculiar thickening of the cell-walls, with the formation of bars or striæ, occasionally met with in old *prothallia*.
- Fig. 20. *Antheridium*, seen by looking down upon it.
- Fig. 21. Side view of an *antheridium*, in which the protoplasm is just beginning to subdivide to form the *sperm-cells*.
- Fig. 22. A more advanced specimen.
- Fig. 23. Nascent *sperm-cells*, from the preceding figure.
- Figs. 24-26. *Antheridia*, seen from above, showing the subsequent stages of development of the *sperm-cells*. In figs. 24 & 25 the annular enveloping cell is still perceptible; in fig. 26 its inner membrane is pressed out and applied against the outer one, and invisible.
- Figs. 27-29, 31, 32. Various stages of development of marginal *antheridia* from young *prothallia*, produced from buds arising on old sterile *prothallia*.
- Fig. 33. Hairs found near the notch on the under face of perfect *prothallia*.
- Fig. 34. Side view of an *antheridium* distended with perfect *sperm-cells*.
- Fig. 35. *Antheridia*, seen from above, focused to show the condition of the ripe *sperm-cells* within.
- Fig. 36. An *antheridium*, burst by pressure, emitting its *sperm-cells*.
- Fig. 37. *Sperm-cells*, one with a nucleus, before the spiral filaments or *spermatozoids* are perceptible in them.
- Fig. 38. Side view of an *antheridium*, with the *spermatozoids* escaping freely, bursting the *sperm-cells* within the cavity of the *antheridium*.
- Fig. 39. *Sperm-cells*, not quite ripe, exhibiting the *spermatozoids* coiled up in them.
- Fig. 40. *Spermatozoids* in motion, seen in different positions; the halo of light around each is the result of the movement of the cilia, which is so rapid that they are invisible.
- Fig. 41. *Spermatozoids*, arrested by solution of iodine, exhibiting the cilia.
- Fig. 42. Peculiar conditions of the *spermatozoids*, seen in one instance only: the left-hand figure represents one uncoiled; the right-hand one appears to have a capillary tail, since it dragged the little mass of mucilage represented along with it.
- Figs. 43 & 44. *Spermatozoids*, imperfectly developed and incapable of extricating themselves from the *sperm-cells*, but seen in motion.

- Fig. 45. Drawing representing the presumed character of a perfect *spermatozoid*, derived from the examination of numerous specimens.
- Fig. 46. Imperfect *spermatozoids*.
- Fig. 47. Other forms, where the coils were distinct, but which were sketched while in motion, so that the cilia were not seen.
- Fig. 48. Side view of an *antheridium* after it had discharged its *spermatozoids*. The lid is still attached, but the internal membranes have acquired a brown colour.
- Fig. 49. Another specimen from which the lid has been wholly detached.
- Fig. 50. Portion of a proliferous old *prothallium* with marginal, mostly effete, *antheridia*.
- Fig. 51. Slightly magnified view of the under side of a perfect *prothallium*, in which the cushion-like thickening has been developed.
- Fig. 52. Magnified view of the region near the notch on the lower surface of a similar *prothallium*, bearing *archegonia* in various stages.
- Fig. 53. More enlarged view of a smaller portion with several sterile *archegonia*.

TAB. XVI.

- Fig. 54. View of a nascent *archegonium* focused to the (under) surface of the *prothallium*. At *a* is the cell of the general surface overlying the *embryo-sac*, which is seen through, as are the cells bordering it, marked *b*.
- Fig. 55. The same preparation focused deeper so as to show the *embryo-sac*, *a*, and its boundary cells, *b*.
- Fig. 56. A similar view to fig. 54, where the cell above the *embryo-sac* already exhibits cross lines, indicating its division into three, preparatory to growing out into the papilla; *c* shows the cellule (*embryonal vesicle*), with a nucleus formed in the *embryo-sac*; *b*, the boundary cells.
- Fig. 57. The same figure focused deeper: *a*, the *embryo-sac*; *b*, its boundary cells; *c*, the *embryonal vesicle*.
- Fig. 58. Lateral views of *archegonia*, showing the gradual development of the papilla.
- Fig. 59. More advanced papillæ before the canal is visible.
- Fig. 60. Similar papillæ seen from above.
- Fig. 61. Lateral view of an *archegonium* in which the canal of the papilla is becoming evident.
- Fig. 62. Vertical section through the thickness of the cushion-like mass of the *prothallium*, passing in various situations through *archegonia*.
- Fig. 63. Vertical section of two *archegonia*, one of which exhibits the mucilaginous filaments hanging out from the canal.
- Fig. 64. Vertical section passing through four *archegonia*; *b*, the cells bounding the *embryo-sac* of one of them.
- Figs. 65 & 66. Vertical sections of *archegonia*, passing through the canals and *embryo-sacs*.
- Fig. 67. Vertical section of a portion of a *prothallium* passing through two *archegonia*.
- Fig. 68. More highly magnified view of three *archegonia*, differently focused; the side one shows the canal through the transparent walls; the middle displays the *embryo-sac* and *embryonal vesicle* showing through.
- Figs. 69 & 70. Views of *archegonia* obtained without sections, focused to show the contents of the canals and *embryo-sacs*, distinguishable through the transparent walls.
- Fig. 71. Vertical section passing through two *archegonia*; the left figure appears to be of one just fertilized, the right figure exhibits merely the base of a dead *archegonium*.
- Figs. 72 & 74. Views of dead abortive *archegonia*, with the walls of the widely-opened canals and the *embryo-sacs* coloured deep brown.

